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MORPHOLOGICAL INTEGRATION IN THE SKULL OF *DISCOSAURISCUS AUSTRIACUS* (MAKOWSKY, 1876) (BATRACHOSAURIA, SEYMOURIAMORPHA) FROM THE LOWER PERMIAN OF CENTRAL EUROPE [1]

(With 3 figures)

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ABSTRACT: Two models of morphological integration (static allometry and geometric orientation) in the skull of the amphibian *Discosauriscus austriacus* were compared by means of maximum-likelihood factor analysis, performed on the correlation matrix among 14 morphometric variables measured in the skulls of 70 specimens of *D. austriacus* from the Boskovice Furrow site (Lower Permian of Czech Republic). The ordination of the correlation matrix depicted two groups of variables with common variation patterns, comprising the variables included in the geometric orientation model and corresponding to different zones of morphological integration in the skull. The fit of the static allometry model was not acceptable, suggesting the influence of other factors besides the overall size on cranial growth in *D. austriacus*. The fit of the models of integration based on geometric orientation (skull width x skull length) was statistically acceptable for skull width only, suggesting the action of distinct morphogenetic fields in the determination of patterns of cranial morphological integration patterns in this species.

Key words: multivariate morphometrics, factor analysis, integration models, Discosauriscidae, Amphibia.

RESUMO: Integração morfológica no crânio de *Discosauriscus austriacus* (Makowsky, 1876) (Batrachosauria, Seymouriamorpha) do Permiano Inferior da Europa Central.

Dois modelos de integração morfológica (alometria estática e orientação geométrica) no crânio do anfíbio *Discosauriscus austriacus* foram comparados mediante a análise fatorial confirmatória pelo método de máxima verossimilhança, efetuada sobre a matriz de correlação entre 14 variáveis morfométricas tomadas em crânios de 70 espécimes de *D. austriacus* obtidos do sítio de Boskovice Furrow (Permiano Inferior da República Checa). A ordenação da matriz de correlação revelou dois grupos de variáveis com padrões de variação comuns, compreendendo as variáveis incluídas no modelo de orientação geométrica e correspondendo a diferentes zonas de integração morfológica no crânio. O ajuste do modelo de alometria estática não foi adequado, indicando a influência de outros fatores além do tamanho geral sobre o crescimento craniano de *D. austriacus*. O ajuste dos modelos de integração baseados na orientação geométrica (largura x comprimento do crânio) foi estatisticamente adequado apenas para a largura do crânio, sugerindo a ação de campos morfogenéticos distintos na determinação dos padrões de integração morfológica craniana nesta espécie.

Palavras-chave: morfometria multivariada, análise fatorial, modelos de integração, Discosauriscidae, Amphibia.

INTRODUCTION

It has long been known that the vertebrate skull is not a compact, homogeneous structure throughout the developmental process of an organism. OLSON & MILLER (1958) coined the term "morphological integration" to describe the interdependence and coordination among the different morphological parts of an organism during development. According to these authors, levels of morphological integration could be recognized by the patterns of statistical correlations among morphometric variables, with highly correlated morphological structures representing true integrated and biologically functional groups.

Studies of morphological integration have been carried out in several groups of recent vertebrates, especially mammals and reptiles, using multivariate statistical techniques (GOULD & GARWOOD, 1969; DODSON, 1975; ZELDITCH, 1987, 1988; ZELDITCH & CARMICHAEL, 1989; ROTH, 1996; MONTEIRO, 1997). However, very few investigations of morphological integration have been carried out in fossil groups (OLSON & MILLER, 1958;

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GOULD, 1967), mainly because of the relative difficulty of obtaining less pressure-deformed material and sample sizes large enough to allow exact measurements and meaningful statistical analyses of the data.

Discosauriscus austriacus (Makowsky, 1876) is an amphibian of the Lower Permian of Central Europe (France, Germany, and Czech Republic) and the Upper Permian of Russia. According to CARROLL (1988), the discosauriscids are known only from larval or neotenic forms. Using the multivariate statistical technique of principal components analysis, KLEMBARA & JANIGA (1993) found that the length of skull increases during growth in *D. austriacus* at a greater relative rate than the skull width, suggesting the existence of integrated morphological complexes in the skull of this species.

In the present study, confirmatory factor analysis (NEFF & MARCUS, 1980; ZELDITCH, 1987; MORRISON, 1990) was used to investigate the levels of integration among cranial quantitative variables in *D. austriacus*, in an attempt to contribute to the understanding of morphological developmental patterns in this species.

MATERIAL AND METHODS

The original data from KLEMBARA & JANIGA (1993), consisting of 14 morphometric variables (Tab.1) measured in the skulls of 70 specimens of *D. austriacus* from the Boskovice Furrow site in Moravia (Lower Permian of Czech Republic), were used for the analysis.

Maximum-likelihood confirmatory factor analysis (NEFF & MARCUS, 1980; MORRISON, 1990) was performed on the correlation matrix computed among the 14 morphometric variables. This analysis was employed to search for patterns of variation in the skulls of *D. austriacus* that could define complexes of interrelated variables, by testing different models (hypotheses) of morphological integration (ZELDITCH, 1987). Two models of integration were evaluated: a simple growth (static allometry) model and a complex factor (geometric orientation) model (Figs.1, 2). These models specify the latent variables (factors) and their influence on observed variables (morphometric variables). The fit of each model was evaluated by means of a x^2 test, with a nonsignificant value implying an acceptable fit of the model to the observed data, at the fixed significance level. A stringent significance level ($\alpha < 0.001$) was used to avoid adopting unnecessarily complex models (ZELDITCH, 1987).

The static allometry model asserts that the only factor of integration is the common tendency of all measures to increase during growth. The geometric orientation model, in turn, predicts the existence of highly integrated functional groups among morphometric variables sharing a common geometric orientation; according to this model, the length and width measures would form discrete integrated units with different growth patterns along development (ZELDITCH, 1987).

In factor analysis, it is usual practice to rotate (by several criteria) the factor axes after an initial solution is reached, in order to maximize the factor correlations with the most important variables in their composition and obtaining a final solution that shows "simple structure". In this study, factors with associated eigenvalues larger than unity were extracted for each model and rotated to simple structure by the Varimax method (NEFF & MARCUS, 1980; MORRISON, 1990).

TABLE 1
Morphometric variables measured on the skull of each specimen of *Discosauriscus austriacus*

Variable	Description
V1	Parietal foramen-postparietal
V2	Width of skull table at mid-supra temporal
V3	Length of parietal
V4	Width of parietals
V5	Length of frontal
V6	Length of nasal
V7	Width of nasal
V8	Connecting line of lateral tips of prefrontals
V9	Interorbital width●
V10	Connecting line of level 9■ - nasal
V11	Connecting line of orbit▲ - postparietal
V12	Length of postparietal
V13	Connecting line of lateral tips of postfrontals
V14	Squamosum◆

(●) interorbital width is measured at level of contact of prefrontal with postfrontal; (■) this connecting line is measured from level at which interorbital was measured; (▲) orbit is measured from its anterior margin; (◆) connecting line between posteromedial and posterolateral tips of squamosum.

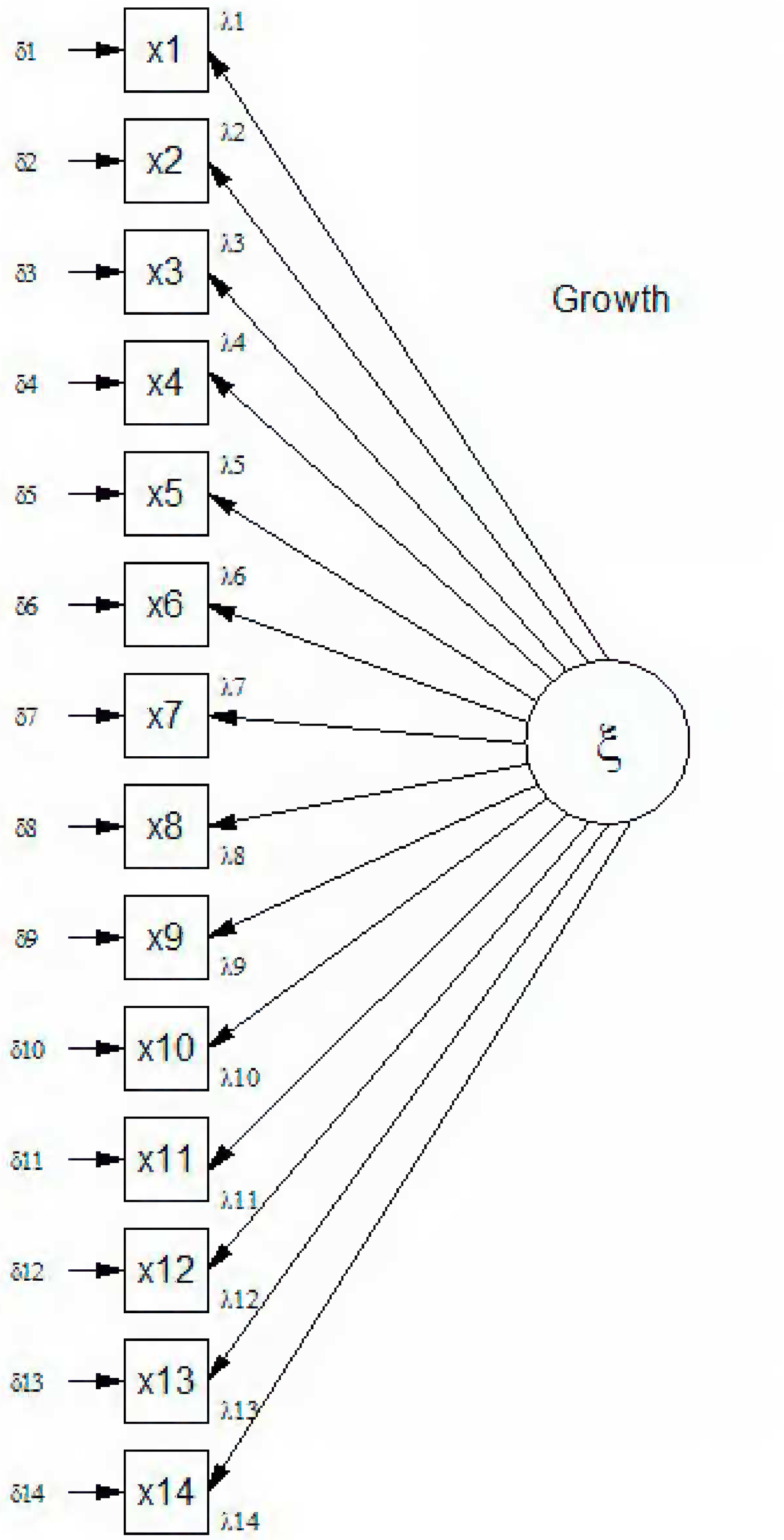

Fig.1- Path diagram for the static allometry model. Squares represent the observed morphometric variables, latent variables (factors) are enclosed in a circle, and arrows represent the direction of the causal influence.

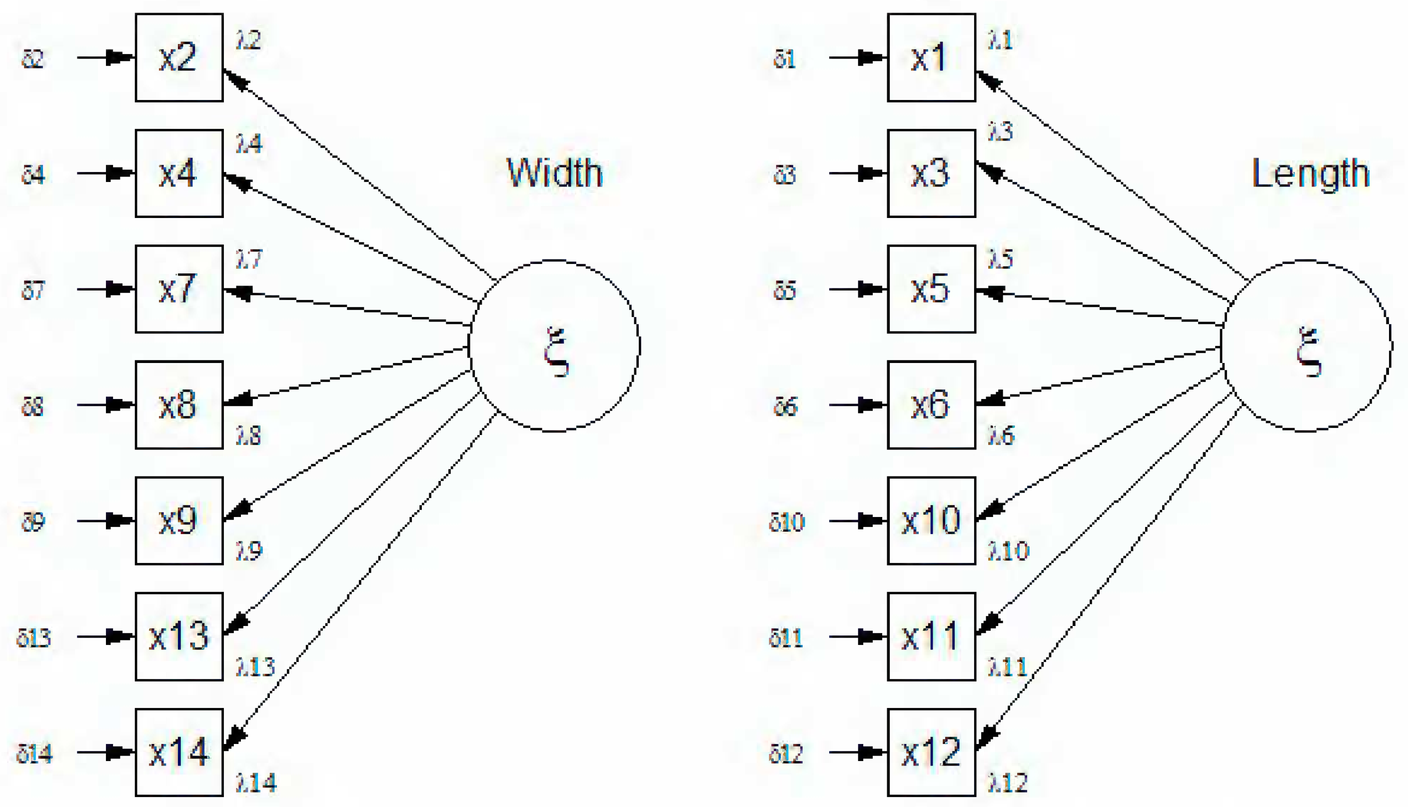

Fig.2- Path diagrams for the geometric orientation model. Squares represent the observed morphometric variables, latent variables (factors) are enclosed in circles, and arrows represent the direction of the causal influence.

All computations were performed with an IBM-PC compatible microcomputer using the STATISTICA package, version 4.3 (STATSOFT, 1993).

RESULTS AND DISCUSSION

The ordination of the correlation matrix among variables depicted two groups of morphometric variables sharing common variation patterns (Fig.3). Each group comprised the variables included in the two models of geometric orientation, corresponding to different zones of morphological integration in the skull of *D. austriacus*.

The fit of the static allometry model (that accounted for about 74.1% of the total variation) was not statistically acceptable, suggesting the influence of factors other than general size on the covariation of skull variables in *D. austriacus*. The fit of models of integration based on geometric orientation (skull width and length, that accounted for 75.7% and 68.8% of the total variation, respectively) was acceptable

TABLE 2

Goodness-of-fit test of the static allometry and geometric orientation (width and length) models of integration

Model	%	χ^2	df	P
Static allometry	74.1	174.97	76	0.000000
Width	75.7	31.71	14	0.004414
Length	68.8	70.47	14	0.000000

The null hypothesis is that all off-diagonal elements in the residual correlation matrix are equal to 0 (df=degrees of freedom).

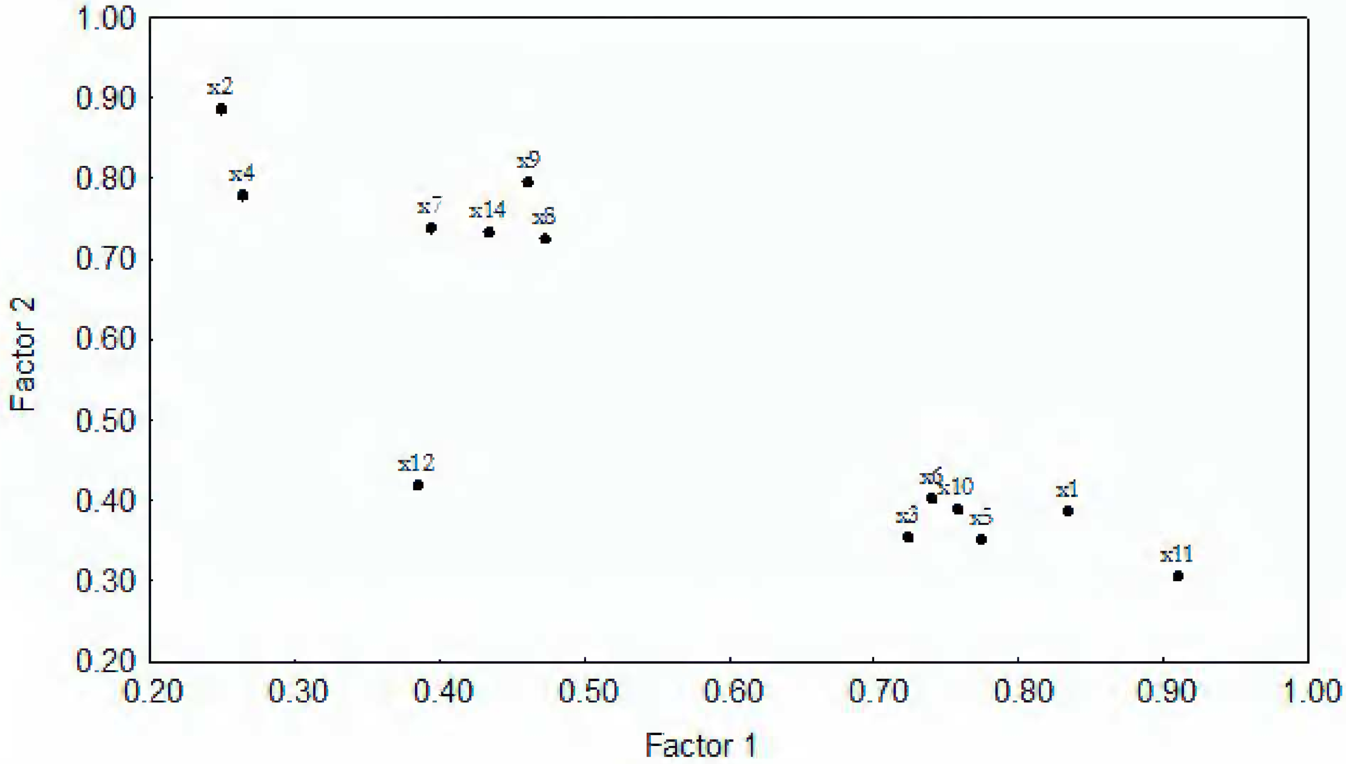

Fig.3- Projection of the 14 morphometric variables on the reduced space of the two Varimax-rotated factors extracted from the correlation matrix among variables. Variable 13 is overlapped by variable 14 and is not displayed.

for skull width only (Tab.2). While all evaluated models accounted for an appreciable proportion of morphological integration in the skull of *D. austriacus*, their relative lack of fit to the structure of the correlation matrix among variables suggests that the original matrix presents a more complex covariation structure than that accounted for by any of the proposed models.

These results are consistent with the existence of integrated complexes of morphological variables in the skull of *D. austriacus* and provide additional support for the findings of KLEMBARA & JANIGA (1993) with respect to the differential rates of cranial growth, suggesting the action of distinct morphogenetic fields in the determination of patterns of cranial morphological integration in this species. Nonetheless, a better understanding of these patterns will have to await for a detailed study, employing more complex integration models based on the cranial development of the Amphibia and including a larger number of latent variables.

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